SPRING BEHAVIOR OF *POLISTES EXCLAMANS* (HYMENOPTERA: VESPIDAE: POLISTINAE)[1]

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ABSTRACT: *Polistes exclamans* most often is haplometrotic in its nest founding. Yet, pleometrotic nest founding appears to result in a greater reproductivity. Nest founding commences after intermittent movements back and forth from their winter hibernaculum. Periods of slow and rapid nest enlargement are evident because of the presence of a single founding female.

Polistes exclamans (Vierech), commonly known in Georgia as the Guinea Wasp, is generally a haplometrotic species, second in apparent abundance in the Athens area to *Polistes annularis* (L.) (Hermann and Dirks 1975). On occasion, more than one female founds a nest, resulting in some behavioral difficulties.

The behavior of *P. exclamans* has been studied extensively, the latest accounts of which are those of Eberhard (1969), Eickwort (1969), Gillaspy (1973), Rabb (1960) and West (1968). Our study primarily was undertaken during the spring and early summer of 1975, although scattered observations on this species have been made for several years.

Materials and Methods

A total of 33 nests were observed over a 10-week period. Observation sites included storage buildings, barns, vacant houses, beneath eaves and awnings of houses, carports, porches and building entrances. Nests and wasps were marked in the same manner as that outlined by Hermann and Dirks (1975).

Results and Discussion

Post-Hibernation Behavior

Following the hibernation of fertile females (Hermann, Gerling and Dirks 1974), individuals of *P. exclamans* emerge from their hibernaculum about mid-April. Selection of a nest site begins at

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this time, although the females of this species intermittently return to their hibernaculum until warm weather prevails. Most nests were initiated during the last week of April. Even after the initiation of nest building, females of *P. exclamans* enter their hibernaculum on cool nights and return to their nest when the temperature rises. We found no pre-nesting aggregations in this species as was found for *P. annularis* (Hermann and Dirks 1975). At the time of nest initiation by *P. exclamans*, *P. annularis* is most often already a month into colony founding (Hermann and Dirks 1975) in the Athens area.

The slowness with which colony founding takes place may be due to the haplometrotic behavior of the founding queen. The prenesting aggregations found in posthibernating *Polistes annularis* females apparently stimulates the regrouping of sibling females and the initiation of nest-building behavior. Such prenesting behavior is absent in *P. exclamans*.

Nest Initiation and Foundress Associations

Of the 33 nests observed in 1975, only two were attended by more than one female; on each of these two nests were two foundresses. During the spring of 1974, following an unusually warm winter (Hermann, Gerling and Dirks (1974), Krispyn (1975) observed up to four females on a single nest. West (1968) observed more than one foundress on nests of *P. exclamans* in Texas but found only single foundresses of this species in other areas (Oklahoma, Kansas).

Of the two nests founded by two foundresses in our study area in 1975 one female left her nest shortly after initiation while the second nest remained occupied by two females for almost two weeks. Of all observations for several years on *P. exclamans*, we have never seen colony founding continue for more than two weeks with more than one female.

During the period in which both females occupy the same nest the distinction between dominant and subordinate females is evident; one female moves around the face of the nest and assumes a dominant posture in encounters with other wasps while the other female remains chiefly on the side of the nest and demonstrates a distinctly subordinate "crouching" posture.

Nest Growth and Survival

Many nests of *P. exclamans* are unsuccessful, possibly due to the presence of a single founding queen. Of the 33 nests observed in 1975, 14 were abandoned between 1-6 weeks after colony initiation. If pleometrosis were practiced by this species there is a possibility that the success of each nest would be more likely. Most *P. annularis* nests that become defunct are founded by a single female.

Pleometrosis, therefore, appears to be an advantage to social insects and likely to be developed in more species with time. However, Michener (1964) indicated that haplometrosis is a beneficial condition in social insect colonies by pointing out the fact that a greater reproductivity per female is attained in haplometrotic colonies. Subsequently, Spradbery (1971) stated that greater reproductivity per female may be responsible for the presence of haplometrotic colonies in eusocial insects. This may not be the case, however, as we will point out in the following paragraphs.

Later survival of this species in the Athens area depends largely on the prevalence of parasites and on predation by the summer tanager, *Piranga rubra.* On several occasions Krispyn (1975) has witnessed the complete destruction of *P. exclamans* and *P. metricus* nests by these birds. A bird hovers by the nest, sometimes grabbing adult wasps in its beak. Some adult wasps escape and the bird then pecks at the nest and feeds on wasp immatures, resulting in a shredding of the nest and termination of the colony. We also have seen nests of *P. annularis* that were riddled and torn in this fashion.

Successful *P. exclamans* nests showed a steady growth until the nests had 5-8 capped cells (Table I). At this point the queen appeared to concentrate on the care and feeding of the remaining larvae. Nest construction slowed considerably. The data in Table I points out early rapid nest growth (through May 18), a slow period (May 20-June 11) and a period of increased nest construction (June 15) after the emergence of the first workers. Compared to Table II for *P. annularis* in the spring of 1970 we may point out several similarities and differences between the two species. Time of colony initiation should not be correlated since weather factors were different in each case: 1) more cells are produced per nest by *P. annularis,* although more cells per female are produced by *P.*

exclamans; 2) the appearance of capped cells takes about the same length of time in both colonies; 3) the length of time for the emergence of adults is much the same in both colonies; 4) there is not as obvious a decrease in cell building in *P. annularis* colonies as there is in colonies of *P. exclamans;* 5) at the time of worker emergence in both cases there is an immediate increase in cell number. In the latter case, however, 30 cells are present at the onset of new cell building by *P. exclamans* workers (June 15, Table I), whereas 80 cells are present in colonies of *P. annularis* (June 16, Table II). In spite of the very distinct dominance-subordination reactions on a *P. exclamans* nest founded pleometrotically, Krispyn (1975) has shown that such nests grow very much more rapidly than haplometrotic ones.

It is apparent, then, with more cells per nest and less of a decrease in cell building after the first caps appear in nests of *P. annularis,* that nests of *P. exclamans* suffer in worker output because the species is haplometrotic.

TABLE I.

AVERAGE DATA FROM 10 *P. EXCLAMANS* NESTS WITH ONE FOUNDRESS (ATHENS, GEORGIA, 1975).

Date	#of cells present	# of capped cells	# of workers
April 24	3	–	–
29	7.2	–	–
May 4	12.7	–	–
10	19.0	–	–
12	19.8	.1	–
13	20.1	1.4	–
14	20.4	3.7	–
16	21	4	–
18	21.5	4.3	–
20	22	5	–
22	22.3	5.7	–
24	22.5	5.7	–
26	22.9	6	–
28	23.3	6	–
30	23.4	6.6	–
June 1	23.8	7.5	–
5	24.1	7.6	–
7	24.6	7.9	–
11	25.3	7.7	.4
15	30.2	5.2	3.6

TABLE II.

AVERAGE DATA FROM THREE *P. ANNULARIS* NESTS (1970) WITH AN AVERAGE OF 2.3 COFOUNDRESSES PER NEST (FROM HERMAN AND DIRKS 1975).

Date	# of cells present	# of capped cells	# of workers
April 16	13.33	–	–
17	14	–	–
18	16	–	–
22	21	–	–
23	24	–	–
26	24	–	–
May 1	32.33	–	–
13	41.5	0.33	–
20	44.33	8	–
22	46	11.33	–
27	50	16	–
June 16	80	14	16
17	–	13.5	13.5

Tail Wagging

Rapid movement of the gaster by the queen is evident in early colony life by *P. exclamans* and demonstrated to a lesser degree by workers. Such movements, known as tail wagging (Eberhard 1969, Hermann and Dirks 1975), are usually thought of as a demonstration of hierarchical dominance (= peck order, dominance-subordination relationship); since *P. exclamans* is generally haplometrotic in its nest founding it is difficult to understand what the function of tail wagging is in early nest founding in this species. It may play a role in the later establishment of a dominance hierarchy among the workers of the colony, possibly in the determination of what workers will lay eggs for the production of males late in colony life.

Tail wagging in colonies of *P. annularis* (Hermann and Dirks 1975) appears to produce several important results: 1) it establishes the whereabouts of the dominant female and subordinate cofoundresses; 2) it appears to assist the dominant female in maintaining her position in the hierarchy; 3) it appears to increase nest acitivity either audibly or visually 4) it indicates that workers enter the dominance reactions and succeed in holding a dominant position over subordinate cofounding females.

There is also the possibility that pheromones or defensive compounds may be produced in the abdomen (Hermann and Dirks 1974) and dispersed with the lateral wagging movements. This possibility has not been investigated although it offers a reasonable explanation for tail wagging in a haplometrotic female.

Aggression and Colony Protection

Unlike the queens of *P. annularis*, those of *P. exclamans* do occasionally attack an intruder without much provocation. We have been aggressively approached by a *P. exclamans* queen from a distance of 18 feet from the nest.

Attack by workers after provocation often is not *en masse* but by a single individual. Threatening posture of raised abdomen and fluttering wings, as described by Eberhard (1969) is commonly demonstrated by the queen and workers.

When group stinging was evident it appeared that nest vibrations, initiated by alarmed individuals, alerted other workers on the nest. This means of communication also was reported by Eberhard (1969). When disturbance was enough to cause a group exodus from the nest the first individual to return to the nest was the queen.

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